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The Direction of Walking—but Not Throwing or Kicking—Is Adapted by Optic Flow

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Abstract

Optic flow is known to adapt the direction of walking, but the locus of adaptation remains unknown. The effect could be due to realignment of anatomical eye, head, trunk, and leg coordinate frames or to recalibration of a functional mapping from the visual direction of the target to the direction of locomotor thrust. We tested whether adaptation of walking to a target, with optic flow displaced by 10°, transfers to facing, throwing, and kicking a ball to the target. A negative aftereffect for initial walking direction failed to transfer to head orientation or throwing or kicking direction. Thus, participants effectively threw or kicked the ball to the target, and then walked in another direction to retrieve it. These findings are consistent with recalibration of a task-specific visuo-locomotor mapping, revealing a functional level of organization in perception and action.

Keywords

perception and action; locomotion; human

A process of perceptual-motor calibration is essential to keep everyday actions coordinated with environmental targets. Without such calibration—in situations in which perceptual feedback is removed—goal-directed movements drift over time and lose precision and accuracy (Bingham & Pagano, 1998; Vindras & Viviani, 1998). Presumably, the perceptual-motor mappings that underlie adaptive behavior are maintained by continuous calibration throughout life (Bingham, Coats, & Mon-Williams, 2007).

We recently demonstrated that optic flow serves as a “teaching signal” to adapt the mapping between the visual direction of a goal and the direction of walking (Bruggeman, Zosh, & Warren, 2007). During adaptation, participants repeatedly walked to a target in a textured virtual environment while the heading direction specified by optic flow (virtual heading) was displaced by 10° to the right of their actual walking direction (locomotor axis). On the first few trials, the virtual heading at the onset of walking missed the target by a comparable amount (~10°), leading to a curved path (Fig. 1). But after several trials, this initial virtual heading error was reduced by half, even though participants were unaware of the error. In the test phase, when the heading displacement was removed and the target was a single line in a dark field, we observed a negative aftereffect in the initial walking direction (about 4°–5° to the left), which led to a significantly curved path in the opposite direction that revealed the adaptation (Fig. 1).

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Two of our findings are critical. First, optic flow appears to be essential for adaptation of the initial walking direction, as adaptation occurred only in a visually structured environment with rich optic flow, not in a sparse environment with the target alone. Optic flow ordinarily specifies the direction of travel through the environment (Gibson, 1950; Warren, 2007), and thus provides a reliable teaching signal for locomotor adaptation. Second, contrary to previous suggestions (Rushton, 2004; Rushton & Salvucci, 2001), the adaptation cannot be ascribed to a shift in the visual straight-ahead. Participants were instructed to face the target at the beginning of each trial, and their head orientation did not show any sign of adaptation.

What, then, is the locus of adaptation? Two hypotheses are suggested by the literature (Redding, Rossetti, & Wallace, 2005; Rieser, Pick, Ashmead, & Garing, 1995). First, the *anatomical hypothesis* proposes that adaptation is due to proprioceptive realignment of the eye-head, head-trunk, or trunk-legs coordinate frames (or some combination of these frames), and that this realignment alters coordinate transformations between body segments. Second, the *functional hypothesis* proposes that optic flow recalibrates a task-specific mapping from the visual direction of the target to the direction of locomotor thrust.

The anatomical hypothesis stems from prism adaptation studies of pointing to a visual target (C.S. Harris, 1963; Redding & Wallace, 1997). A participant wearing laterally displacing prisms exhibits a rapid adaptation of pointing direction in the absence of changes in gaze direction (Bingham & Romack, 1999). The adaptation in pointing direction transfers to auditory targets and is attributed to a realignment of the felt position of the arm relative to the head. It is accompanied by a more gradual adaptation of the visual straight-ahead, which is attributed to realignment of the felt eye position relative to the head (Hay & Pick, 1966b).

Analogously, optic flow might serve to realign the proprioceptive coordinate frames of body segments during locomotion. The initiation of walking to a visual target involves a transformation of the visual direction of the target from oculocentric to headcentric, bodycentric, and effector coordinate frames. Thus, optic flow might adapt eye-head, head-trunk, or trunk-legs coordinate transformations. We have already shown that the eye-head frames are not realigned, because head orientation to face the goal is unaffected by locomotor adaptation (Bruggeman et al., 2007). However, a realignment of the head-trunk or trunk-legs frames could account for adaptation of the initial walking direction.

Alternatively, optic flow might serve to recalibrate a functional mapping from the target's visual direction to the direction of locomotor thrust. We call such a perceptual-motor relation a *control law* (Warren, 1988, 2006), a task-specific mapping from an informational variable to a control parameter that governs forces for a class of actions. A control law for steering is functionally specific to the task of locomotion, not anatomically specific to particular body segments, and may apply to any goal-directed displacement of the body regardless of the effectors involved. Although the mapping depends on proprioceptive relations among body segments, according to this view they are not the sites of adaptation. Of course, it is possible that both anatomical realignment and functional recalibration occur during locomotor adaptation.

In the study reported in this article, we tested the anatomical and functional hypotheses by determining whether the adaptation of initial walking direction transfers to other goal-directed actions performed with the head, trunk, and leg segments: (a) facing a distant target, (b) throwing a ball to the target, and (c) kicking a ball to the target. If the locus of adaptation is realignment of the eye-head coordinate frames, the negative aftereffect for walking should transfer to all three tasks, but our previous data are inconsistent with this hypothesis (Bruggeman et al., 2007). If there is a head-trunk realignment, the aftereffect should transfer to throwing and kicking, but not facing the target. And if there is a trunk-leg realignment, it

should transfer only to kicking. In contrast, if the locus of adaptation is a task-specific control law, the aftereffect for walking should not transfer to any of the nonlocomotor tasks. Surprisingly, this would create a situation in which participants effectively throw or kick a ball to the target, and then walk in a different direction to retrieve it.

Method

Participants

Sixteen participants (5 females and 11 males) with normal or corrected-to-normal vision participated in the experiment. They ranged in age from 18 to 28 years ($M = 21.1$ years, $SD = 2.6$). None of them had any previous experience in this kind of study. Subjects gave informed consent in accordance with the human-subjects policies of Brown University.

Materials

Participants walked freely in the 12 m $\times$ 12 m Virtual Environment Navigation Lab at Brown University while wearing a head-mounted display, which presented stereo images generated at 60 Hz with a 63° (horizontal) $\times$ 53° (vertical) field of view (a shield blocked all peripheral vision, including downward vision). Head position and orientation were recorded at 30 Hz and used to update the display with a latency of 70 ms. In the *line environment*, used on pre- and posttest trials, the target was a vertical red line in a dark field; the line, which had a diameter of 0.008 m, ran off the top and bottom of the display. In the *texture environment*, used on adaptation trials, the target was a doorway that was 0.5 m wide and positioned in a frontal wall of a virtual room with a ground plane and ceiling; these surfaces were mapped with a gray-scale random-noise texture. In addition, an array of vertical textured posts (0.05 m in diameter) was randomly positioned on the ground, with approximately 19 posts visible in the first frame. This visually structured environment provided rich optic flow, including motion parallax and target drift, to a walking participant.

The *virtual heading* was dissociated from the physical heading by displacing the simulated direction of travel through the virtual environment by 10° to the right (or left) of the participant's actual direction of walking in the physical environment, as in our previous study (Bruggeman et al., 2007). Thus, an observer walking in the egocentric direction of the target would see an optic-flow pattern that specified a heading 10° to the right of the target, equivalent to a virtual heading error of +10° (or a pattern that specified a heading 10° to the left of the target, an error of -10°). Steering so as to place the visually specified heading (e.g., the focus of expansion in the optic-flow pattern) on the target would bring the virtual heading error to 0°.

Design and procedure

A pretest-adaptation-posttest design was used. During the 38 *adaptation trials*, the virtual heading was displaced by 10° from the actual walking direction; for half of the participants, it was displaced to the right (+10°), and for the other half, it was displaced to the left (-10°). At the beginning of each trial, participants positioned themselves at a starting post, turned to face a distant marker, and began walking when the marker disappeared and the texture environment appeared; the target doorway was at an initial distance of 9 m. Participants were instructed to walk at a normal pace on the most direct path to the target and to walk through any posts that obstructed their way; the environment remained visible throughout each trial, providing continuous (error) feedback.

During the 8 *pretest* and 8 *posttest trials*, the optical displacement was removed, and the (initial) direction of throwing, kicking, walking, and head orientation was assessed. On each trial, the line environment appeared with the target line at an initial distance of 9 m.

Participants first threw a 0.150-kg lacrosse ball underhand toward the target (essentially rolling the ball on the ground) and then kicked a 2-kg rubber ball toward the target (using the sole of their foot to roll the ball on the ground, while holding a walking stick to help maintain balance). Finally, the target line disappeared, and they walked toward its location for about 5 m. Just prior to the onset of walking on every trial, participants were instructed to face the target, and head orientation was recorded. Participants could not see the ball (the experimenter placed it in their hand or under their foot) and did not receive any visual feedback during pre- and posttest trials (between trials, the experimenter led participants to the start position of the next trial). Prior to the experiment, participants received 5 practice trials in the line environment (without the optical displacement) to familiarize themselves with the throwing, kicking, and walking procedure. The research protocol was approved by Brown University's institutional review board.

Data processing and analysis

To collapse data across the two groups of participants, we converted the head-position data (walking task) and head-orientation data (facing task) of the group with a -10° offset (to the left) to the corresponding values for a $+10^\circ$ offset (to the right). The facing direction prior to walking was measured as the instantaneous head orientation 0.05 s after trial onset (triggered by the disappearance of the distant marker, on adaptation trials, or of the target, on pre- and posttest trials). The head-position data during walking were filtered with a second-order Butterworth filter (0.6-Hz cutoff) to reduce the effects of gait oscillations. The first 0.25 m and last 1 m of each path were removed to eliminate transients, and the intervening temporal samples were normalized in space by binning them into 35 segments, each about 0.23 m in length; these were ensemble-averaged to yield a mean path about 7.75 m long. Path statistics were computed on the segment means and used for analysis of the virtual heading error, which was defined as the angle between the direction of head displacement and the direction of the target. The initial walking direction was computed as the heading error during the 5th and 6th bins (0.38 to 0.45 m from the start). Throwing and kicking accuracy were determined by measuring the point at which the ball crossed a line on the floor immediately behind the virtual target; the lateral distance from the target was converted to an angular error. Like the head-position and orientation data, the throwing and kicking data were collapsed across the two groups of participants; the data of the group with a -10° offset were converted to the corresponding values for a $+10^\circ$ offset.

Data for the initial walking direction during adaptation trials were fitted with a first-order exponential decay function. Post hoc contrasts, based on within-subjects one-way analysis of variance with repeated measures on trial, were applied to test whether the initial walking direction on subsequent adaptation trials differed from that on the first adaptation trial. In addition, pre- and posttest data were used to compute a difference in error between pretest and posttest, and these error differences were analyzed using a within-subjects two-way ANOVA (Task $\times$ Trial) with repeated measures on task and trial. A significant difference in error (i.e., a shift in the direction of movement from pretest to posttest) indicates an aftereffect of adaptation.

Results

Adaptation Phase

During adaptation trials, optic flow was used for both on-line control of locomotion and recalibration of the visuo-locomotor mapping. When the optic flow was displaced to the right of the locomotor axis, walking in the egocentric direction of the target caused the target to drift leftward, yielding a path that curved to the left as the participant “chased” the target. Alternatively, if the participant used the optic-flow pattern to control steering (e.g., by

shifting the focus of expansion onto the target), this would bring the virtual heading error down to zero and yield a straighter path.

Such on-line steering control was evident on the first adaptation trial. The path was much less curved than predicted by the egocentric-direction strategy, and straightened out after the initiation of walking (Fig. 2a). A detailed analysis of the virtual heading error (the angle between the virtual heading and the visual target) over the first trial revealed an early correction (Fig. 2b): Within the first 3 m of walking, following the onset of the optic flow, the virtual heading error dropped from $+10^\circ$ to $+3^\circ$ (reducing the error by about 70%). This early steering adjustment recurred in subsequent trials, even after adaptation of the initial walking direction. This result replicates previous findings (Bruggeman et al., 2007; M.G.Harris & Carre, 2001; Turano, Yu, Hao, & Hicks, 2005; Warren, Kay, Zosh, Duchon, & Sahuc, 2001; Wood, Harvey, Young, Beedie, & Wilson, 2000) showing that people primarily rely on optic flow for the on-line control of locomotion in visually structured environments.

Adaptation was evident in both the reduction of path curvature (Fig. 2a) and the decline in initial heading error (Fig. 2b) over trials. The latter specifically reflects a change in the mapping from target direction to initial walking direction. On the first adaptation trial, participants started walking in the target's egocentric direction, and initial heading error was not statistically different from the predicted value of $+10^\circ$, $t(15) = 1.6$, $p = .14$. But the initial walking direction quickly changed, such that by the fourth trial, the initial heading error differed significantly from $+10^\circ$, $t(15) = 8.8$, $p < .0001$. Over the first 20 adaptation trials, there was a main effect of trial, $F(19, 285) = 2.6$, $p < .0003$, $\eta_p^2 = .15$. Post hoc contrasts (Bonferroni-adjusted p cutoff = .0025) showed that initial heading error on the first trial was marginally different from initial heading error on the third trial ($p = .0026$), and was significantly different from initial heading error on the fourth trial ($p = .001$) and nearly all subsequent trials (median $p = .0021$). Fitting the decreasing initial heading error over trials with a first-order exponential decay function (Fig. 3) revealed an asymptotic value of 4.9° , a 50% reduction from the original 10° displacement (the proportion of variance accounted for, r^2 , was .59).

In contrast, facing direction prior to walking did not change over adaptation trials, but was comparatively stable. The mean head orientation relative to the distant marker was 0.4° ($SD = 1.9^\circ$) for the first five adaptation trials and 0.24° ($SD = 1.7^\circ$) for the last five adaptation trials (Fig. 3). This replicates our previous finding that the visuo-locomotor adaptation cannot be attributed to adaptation of the visual straight-ahead or to realignment of the eye-head coordinate frames (Bruggeman et al., 2007).

Pre- and posttest phases

The data from the pre- and posttests (see Fig. 3) allowed us to evaluate whether adaptation of the initial walking direction transferred to the facing, throwing, or kicking direction. On pretest trials, all four tasks were comparably accurate relative to the target, $F(3, 45) = 0.09$, $p = .96$. The mean directional error was 0.18° ($SD = 2.8^\circ$) for walking, 0.23° ($SD = 2.1^\circ$) for facing, -0.14° ($SD = 3.4^\circ$) for throwing, and 0.28° ($SD = 2.7^\circ$) for kicking. To evaluate the posttest trials for transfer effects of adaptation of the initial walking direction, we computed an error difference score (posttest – pretest) for each task (see Fig. 4).

Initial walking direction shifted by -4.4° ($SD = 2.5^\circ$) on the first posttest trial relative to the pretest (Fig. 4). This shift was significantly different from 0° , $t(15) = 3.1$, $p < .0001$, and demonstrated a large negative aftereffect, corresponding to 86% of the original 5.1° adaptation. In contrast, none of the other three tasks revealed a significant shift on the first posttest trial; the mean shift was 0.33° ($SD = 1.6^\circ$) for facing, 0.45° ($SD = 4.9^\circ$) for

throwing, and 0.94° ($SD = 6.0^\circ$) for kicking. A within-subjects repeated measures ANOVA confirmed that the shifts were significantly different across the tasks, $F(3, 45) = 6.6$, $p = .0008$, $\eta_p^2 = .31$. Post hoc contrasts showed that the shift in walking direction was significantly greater than the shifts for facing, throwing, and kicking, $p < .0001$, $p = .0002$, and $p = .0032$, respectively.

This pattern of results held up across all eight posttest trials, $F(3, 45) = 4.1$, $p = .01$, $\eta_p^2 = .22$. The mean shift in initial walking direction was -3.5° ($SD = 2.5^\circ$), which was significantly different from 0° , $t(15) = 5.7$, $p < .0001$, and corresponded to about 70% of the original adaptation of 5.1° . The other three tasks did not reveal significant shifts; the mean shifts were 0.45° ($SD = 1.4^\circ$) for facing, -0.63° ($SD = 4.7^\circ$) for throwing, and 0.43° ($SD = 4.9^\circ$) for kicking. Thus, the adaptation of initial walking direction decisively failed to transfer to facing, throwing, or kicking direction.

Discussion

The finding that the adaptation of walking direction does not transfer to facing, kicking, or throwing contradicts the anatomical hypothesis. The dissociation of walking from the other three tasks demonstrates that visuo-locomotor adaptation cannot be explained by realignment of eye-head, head-trunk, or trunk-leg coordinate frames. In contrast, the present results are entirely consistent with the functional hypothesis. Specifically, optic flow appears to recalibrate a task-specific mapping from the visual direction of the target to the direction of locomotor thrust. This recalibration is functionally specific to locomotion, does not transfer to other goal-directed actions, and is not mediated by local realignment of anatomical coordinate frames. In effect, after throwing or kicking a ball to the target, participants indeed walked in a different direction to fetch it.

This study replicated our previous findings that optic flow is used for on-line steering control (Warren et al., 2001) and drives visuo-locomotor adaptation, without affecting the visual straight-ahead (Bruggeman et al., 2007). The absence of a shift in facing, throwing, or kicking direction clearly indicates that adaptation of walking direction does not alter the direction of the visual straight-ahead (i.e., perceived egocentric direction). This result counters arguments by Rushton and his colleagues (Rushton, 2004; Rushton & Salvucci, 2001) that steering control relies exclusively on the egocentric direction of the target, and that optic flow plays only an indirect role by influencing perceived egocentric direction. In fact, our study demonstrates the opposite effect: Steering control relies primarily on optic flow in visually structured environments, and the egocentric-direction strategy depends on optic flow to keep the visuo-locomotor mapping calibrated.

Most other studies of the adaptation of walking direction have employed laterally displacing prisms (Brandwood, Rushton, & Charron, 2009; Held & Bossom, 1961; Morton & Bastian, 2004; Redding & Wallace, 1985a, 1985b; Rogers & Spencer, 2005). In contrast to our experiment, such studies have found a partial shift in the visual straight-ahead. Morton and Bastian (2004) found a 5% shift in the visual straight-ahead after 25 trials of walking a 2-m-long path that was marked by two boundary lines, and also reported transfer from walking adaptation to the direction of reaching (30% of prism displacement). Redding and Wallace (1985b) observed that the visual straight-ahead shifted by 9.3% of the prism displacement after 10 min of walking with prisms in a hallway, and Held and Bossom (1961) found a similar 10% shift in the straight-ahead after 2 hr of walking with prisms on a tree-lined path. Note that this magnitude of shift in the straight-ahead (equivalent to 1°) would account for less than a quarter of the shift in walking direction we observed in the first posttest trial (4.4°).

The discrepancy in the literature is likely related to the different methodologies used to create a visual displacement. First, whereas we computed a new direction of travel through the virtual environment, which displaced only the optic-flow pattern, prisms displace the entire visual scene, including both optic flow and the images of objects. Consequently, participants' incidental views of their own limbs or body during prism adaptation could have induced a shift in the visual straight-ahead or reaching direction. Second, whereas our head-mounted display created a symmetrical pincushion distortion that was independent of the optical displacement, lateral prisms create asymmetrical optical distortions that increase with the degree of displacement. Specifically, wedge prism glasses introduce image stretching (during horizontal eye movements) and shearing (during vertical eye movements) that depend on the direction of gaze (Hay & Pick, 1966a; Pick & Hay, 1966), and hence offer a possible basis for eye-head realignment. Despite the reports from prism studies, our finding of a dissociation between walking direction on the one hand and facing, throwing, and kicking on the other establishes the existence of a functional visuo-locomotor mapping that can be recalibrated without adaptation of the straight-ahead or realignment of coordinate frames.

The present results raise the question of whether this recalibration is specific to the act of walking, or might generalize to other forms of overground locomotion. One may hypothesize several levels of organization in perception and action, including a neuromusculoskeletal level defined by particular segments and muscle groups, a biomechanical level defined by joint moments and movement patterns, and a functional level determined by goal-directed forces and outcomes (Bernstein, 1996). A functional class of actions may be characterized by the family of movements that direct forces toward a common perceptually specified outcome, regardless of the particular segments or movements involved (Reed, 1982; Withagen & Michaels, 2005).

Walking, hopping, crawling, swimming, and even rollerboarding with the arms may belong to the same family of locomotor actions because they involve applying directional thrust to displace the body toward a goal, and produce corresponding perceptual information. If so, adaptation of walking direction should transfer to forms of locomotion that involve steering by the application of thrust, but not to locomotion by means of a tricycle with handlebars, a vehicle with a steering wheel, or possibly a skateboard that is steered by leaning. More narrowly, if the action class is defined by the directional displacement of the center of mass relative to the feet, then adaptation of walking should transfer to hopping and sidestepping, but not to crawling. More broadly, if optic flow recalibrates a general mapping between the visual direction of the target and the direction of the locomotor axis, regardless of the manner of force application, then adaptation should transfer to all of these forms of locomotion.

Related evidence for a functional level of visuo-locomotor organization includes experiments in which the *visual gain* of walking was manipulated (Mohler et al., 2007; Rieser et al., 1995; Withagen & Michaels, 2002). Participants adapted to conditions in which the optic-flow rate was visually slower (or visually faster) than the physical walking speed. When transferred to normal conditions and instructed to walk to a target with eyes closed, they overshoot (or undershoot) its distance. This effect transferred from walking to sidestepping and crawling, but not to throwing a ball to the target (Rieser et al., 1995; Withagen & Michaels, 2002). Thus, recalibration of the mapping from visual target distance to walking distance appears to generalize to a family of related locomotor actions, but not to different goal-directed tasks. This pattern of functional dissociation suggests that instead of a single multipurpose representation of space in the brain, there may be multiple perceptual-motor mappings that are specialized for different families of actions (Ingle, 1973).

We conclude that optic flow continually calibrates a task-specific control law for locomotion, specifically, a functional mapping from the visual direction of a goal to the direction of locomotor thrust. These results provide evidence for a functional level of organization in perception and action that is not tied to particular anatomical loci. They imply that optic flow not only plays a direct role in the on-line control of steering, but also plays an indirect role in calibrating the egocentric-direction strategy for steering within a family of locomotor actions.

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Fig. 1.

Adaptation to displaced optic flow and the aftereffect in subsequent walking direction among participants asked to walk toward a target in a textured virtual environment (adaptation) and in an otherwise dark field environment (posttest). The illustration shows a plan view of the mean walking paths on the first (solid blue curve) and last (dashed red curve) of 38 adaptation trials and the first posttest trial (solid black curve). The corresponding vectors starting at the origin of the graph represent the initial walking direction. The path and vector data are taken from Bruggeman, Zosh, and Warren (2007).

Fig. 2.

Results for the adaptation phase: (a) plan view of mean walking paths and (b) mean virtual heading error as a function of walked distance. Results for the first adaptation trial are shown in the solid blue curves, and average results for the last three adaptation trials are shown in the dashed red curves. In (a), the dotted black curve corresponds to the prediction of the egocentric-direction strategy, and the y-axis corresponds to the prediction of the optic-flow strategy. In (b), the dotted black line corresponds to the egocentric-direction prediction of a 10° heading error, and the x-axis corresponds to the optic-flow prediction of a 0° error.

Fig. 3. Direction error on each trial. Results are shown separately for initial walking direction and for kicking, throwing, and facing directions. Participants experienced normal optic flow in the pretest and posttest trials, and displaced (all data converted to $+10^\circ$) optic flow during adaptation. The solid curve represents the exponential fit of the decay in heading error during adaptation, $Y(t)$, with t = the number of the adaptation trial.

Fig. 4. Shift in direction error between pretest and posttest as a function of task. The mean shift in direction error from pretest to the first posttest trial is a measure of the negative aftereffect. Error bars indicate 1 *SE*, based on between-subjects variance.